Thermal Fluctuations in Fluid Membranes 8.334 Final Project

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(Dated: May 17, 2019)

A brief review of mean field theory and differential geometry concepts to introduce models for (fluid) elastic membranes and their fluctuations from nearly-flat or curved zero-temperature configurations. For fluid membranes the bending rigidity and other couplings are only renormalized with the inclusion of nonlinear elastic effects, causing the membrane to become less rigid in the presence of thermal fluctuations. Certain geometrical configurations of the membranes are also found to be unstable to thermal fluctuations, resulting in fragmentation of the membrane into smaller, stable structures. Experiments and simulations inform the relevance of terms in our models, reveal the end products of fluctuation-induced fragmentation, and inspire questions and potential applications for fluid membranes in biology and materials.

I. INTRODUCTION

In our three-dimensional reality, membranes are seemingly the closest nature can come to creating two-dimensional materials. At nonzero temperatures thermal fluctuations are induced in the material which disrupt the flat, ordered state. Eventually fluctuations succeed in destroying the ordered system entirely, through either an abrupt or continuous phase transition. Elastic membranes are well-studied theoretically in arbitrary dimensions for various materials. Simulations and experiments likewise abound, but must combat artifacts of finite lattice/membrane size and laboratory limitations.

Without tethers to an underlying lattice, fluids have continuous shift symmetry and therefore cannot withstand shear forces. This property distinguishes fluids from other elastic membranes, causing them to be quite delicate and more vulnerable to thermal fluctuations. (In certain cases tethering forces can be induced between fluid membranes allowing shears to be sustained. In general, however, the shear modulus $\mu \to 0$.) Consequently, fluid membranes form many interesting structures which would be inaccessible to solids. Amphiphilic molecules self-assemble at the interface of different media to form fluid membranes, aggregate into vesicles and micelles, or generate complex, sponge-like networks.

Fluid membranes are of particular interest for biological systems and applications because of their unique self-assembly, flexibility, and ubiquity. Often in biological contexts the membranes are closed or subject to extrinsic curvatures (either spontaneous or quenched due to defects). It is therefore crucial to understand how thermal fluctuations, chemical properties, and curvature constraints conspire to determine the dynamic behavior and equilibrium configurations of fluid membranes.

In this report we will review mean field theory and differential geometry conventions; construct a model for elastic membranes and impose curvature conditions; determine the effects of thermal fluctuations; and consider ways to experimentally probe our model. We conclude by looking ahead to interesting applications.

II. BACKGROUND

A. Mean Field Theory for Embedded Surface

Let $\vec{r}(\vec{x})$ be a d-dimensional vector (d being the dimension of space in which the membrane is embedded) parameterizing the deformations in space of each point of the membrane, and $\vec{x}=(x_1,x_2)$ the point on the membrane itself. Then for the physical systems of interest, d=3 and $\vec{r}(\vec{x})$ describes both in-plane deformations of the membrane and out-of-plane deformations in the vertical direction.

Changes in the free energy of the membrane will be caused by deviations from the minimal energy equilibrium configuration. These deviations are quantified by the derivatives of \vec{r} at every point on the embedded membrane, i.e. the tangent vector,

$$t_{\alpha}(\vec{x}) = \partial_{\alpha} \vec{r}(\vec{x}) = \frac{\partial \vec{r}(\vec{x})}{\partial x_{\alpha}}$$

with $\alpha \in (1,2)$. We construct a mean field theory for the membrane by writing down all the energy terms which respect the symmetries of the system. Our Hamiltonian must be invariant under translations, rotations, and inversions of the system, and should describe the free energy deviations. Following [1], we choose $t_{\alpha}(\vec{x})$ as an order parameter and write the invariant quantities:

$$\beta \mathcal{H}(\vec{r}) = \frac{1}{2} \int d^2x \left[\kappa (\partial_{\alpha} t_{\alpha})^2 + \tau (t_{\alpha})^2 + u(t_{\alpha} \cdot t_{\alpha})^2 + v(t_{\alpha} \cdot t_{\beta})^2 + \mathcal{O}(t^6) \right]$$
(1)

A sum over repeated indices is implied throughout.

We recover mean field (MF) results for the value of $t_{\alpha}(\vec{x})$ depending on the sign of the (thermal) coupling τ ,

$$|t_{\alpha}^{MF}(\vec{x})| = \begin{cases} 0 & \tau > 0\\ \sqrt{\frac{-\tau}{4(2u+v)}} & \tau < 0 \end{cases}$$
 (2)

indicating a disordered phase for $\tau > 0$ in which the average of the tangent vector is zero, and a flat, ordered

phase when $\tau < 0$ indicating a preferred direction and non-zero average tangent vector.

B. Differential Geometry and Curvature

The language of differential geometry is incredibly useful for studying curved surfaces. In the case of a membrane, curvature is induced by thermal fluctuations or imposed by chemical properties or defects (causing the membrane to be non-flat even at zero temperature). We therefore introduce some differential geometry notation with the goal of describing the membrane's microscopic behavior in terms of global properties such as Gaussian and mean curvatures.

1. Parameterization of a surface

In II A we introduced a Landau-Ginzburg Hamiltonian with $t_{\alpha}(\vec{x}) = \partial_{\alpha} \vec{r}(\vec{x})$ as our order parameter. At zero-temperature, variations in $t_{\alpha}(\vec{x})$ sufficiently describe the extrinsic curvature of the membrane, allowing us to define the metric tensor

$$g_{\alpha\beta}^0(\vec{x}) = \partial_{\alpha}\vec{r}_0(\vec{x})\partial_{\beta}\vec{r}_0(\vec{x}) = t_{\alpha}^0(\vec{x})t_{\beta}^0(\vec{x}) \tag{3}$$

following David's chapter 7 of [2]. (The zero temperature metric is $g^0_{\alpha\beta}$, noting that at finite temperature it becomes perturbed from this form.) If the surface has symmetry, $g^0_{\alpha\beta}(\vec{x})$ could be constant and independent of x, but in general the metric changes from point to point on the membrane. Also there exists everywhere an inverse $g^{\alpha\beta}$ such that $g_{\alpha\beta}g^{\alpha\beta}=1$.

Derivatives on a metric must quantify how the metric itself alters the orientation of a vector. This is accomplished using affine connections,

$$\Gamma^{\alpha}_{\beta\gamma} = \frac{1}{2} g^{\alpha\delta}(\vec{x}) \left(\partial_{\gamma} g_{\beta\delta}(\vec{x} + \partial_{\beta} g_{\delta\gamma}(\vec{x}) - \partial_{\delta} g_{\beta\gamma}(\vec{x}) \right)$$

which define the covariant derivative

$$\nabla_{\beta} X_{\alpha} = \left(\partial_{\beta} X_{\alpha} + \Gamma^{\alpha}_{\beta \gamma} X^{\gamma} \right) \mathbf{e}_{\beta}$$

indicating the covariant derivative is the usual derivative plus an additional term tying the vector to the metric [3].

2. Gaussian, mean, and principal curvatures

To determine extrinsic curvature we construct the shape operator

$$\vec{S}_{\alpha\beta}(\vec{x}) = \nabla_{\alpha}\nabla_{\beta}\vec{r}(\vec{x}) = S_{\alpha\beta}\vec{n}(\vec{x})$$

 $\vec{n}(\vec{x})$ being the normal vector. From $S_{\alpha\beta}$ (the shape operator matrix written in the tangent vector basis) we find

various curvature properties [3]. At any point on the surface $S_{\alpha\beta}$ can be diagonalized such that

$$S_{\alpha\beta} = \begin{pmatrix} \kappa_1 & 0\\ 0 & \kappa_2 \end{pmatrix} \tag{4}$$

where the eigenvalues κ_1 and κ_2 are the principal curvatures which lay along the directions of greatest curvature. It is sometimes useful to use the radius of curvature rather than the principal curvature; the quantities are related by $\kappa_i = R_i^{-1}$. Two more curvatures can be extracted from $S_{\alpha\beta}$:

$$H = \frac{1}{2} \operatorname{Tr}(S_{\alpha\beta}) = \frac{(\kappa_1 + \kappa_2)}{2} = \frac{1}{2} \left(\frac{1}{R_1} + \frac{1}{R_2} \right)$$

$$K = \det(S_{\alpha\beta}) = \kappa_1 \kappa_2 = \frac{1}{R_1 R_2}$$
(5)

H is mean curvature, and K is the Gaussian curvature.

III. MODEL CONSTRUCTION

A. Elastic Hamiltonian

Expanding about the MF flat phase, Eq. 1 is readily recast in terms of the strain tensor $u_{\alpha\beta}(\vec{x})$ and out-ofplane deformations $h(\vec{x})$. Following Nelson's chapter 6.3 of [2] we write the Hamiltonian in Eq. 1 as

$$\beta \mathcal{H}(\vec{r}) = \int d^2x \left[\frac{\kappa}{2} (\partial_{\alpha} t_{\alpha})^2 + \mu u_{\alpha\beta}^2 + \frac{\lambda}{2} u_{\alpha\alpha}^2 \right]$$
 (6)

with μ and λ the Lamé coefficients (μ is the shear modulus). The elasticity coefficients are identified with the MF couplings: $\mu = 4vt^4$ and $\lambda = 8ut^4$ ($t \equiv |t_{\alpha}^{MF}(\vec{x})|$). Note that in the disordered phase ($\tau > 0$) t = 0 so both μ and λ vanish. In terms of t_{α} the strain tensor is:

$$u_{\alpha\beta} = \frac{1}{2} \left(\frac{t_{\alpha} t_{\beta}}{t^2} - \delta_{\alpha\beta} \right). \tag{7}$$

So the Hamiltonian is indeed minimized when $u_{\alpha\beta}=0$, i.e. when the membrane is perfectly flat and there are no in-plane deformations.

Assuming relatively small deformations from this flat phase, we expand the parameter $\vec{r}(\vec{x})$ in terms of the of the in- and out-of-plane deformations

$$\vec{r}(\vec{x}) = t((x_{\alpha} + u_{\alpha}(\vec{x})) \mathbf{e}_{\alpha}, h(\vec{x}))$$

with $u_{\alpha}(\vec{x})$ being the in-plane phonon modes in the \mathbf{e}_{α} direction, and $h(\vec{x})$ the out-of-plane vertical displacements. Then the strain tensor is

$$u_{\alpha\beta}(\vec{x}) = \frac{1}{2} \left(\partial_{\alpha} u_{\beta}(\vec{x}) + \partial_{\beta} u_{\alpha}(\vec{x}) + \partial_{\alpha} h(\vec{x}) \cdot \partial_{\beta} h(\vec{x}) + \partial_{\alpha} u_{\gamma}(\vec{x}) \partial_{\beta} u_{\gamma}(\vec{x}) \right)$$
(8)

and the elastic Hamiltonian is

$$\beta \mathcal{H}(h, \vec{u}) = \int d^2x \left[\frac{\kappa}{2} \left(\partial^2 h \right)^2 + \mu u_{\alpha\beta}^2 + \frac{\lambda}{2} u_{\alpha\alpha}^2 \right]. \tag{9}$$

In the limit that $\mu \to 0$, such as for a fluid membrane, the free energy depends only on the bending modes and the change in area (the trace of the strain).

For long wavelength fluctuations the last term in Eq. 8 is negligible compared to the other terms in the strain tensor, and can consequently be neglected at low temperatures [4]. However, we will see in IVB that this nonlinear term is crucial for renormalizing the fluid membrane.

B. Helfrich free energy

Membranes are formed from surfactants which aggregate at interfaces of media or self-assemble into closed structures to lower the system's free energy [5]. Amphiphilic molecules have hydrophilic heads and hydrophobic tails, so it is energetically favorable for them to arrange such that their heads are dissolved in water while their tails are not [6]. Resulting structures could be nearly-flat mono/bi-layer membranes, micelles, vesicles, microemulsions, or complex combinations of these elements. The density of the membrane is determined by the free energetic balance of attractive surface tension (which tends to shrink the membrane) and packing entropy (which favors more area per molecule).

The stretching modes of a membrane are proportional to change in area (equivalently the strain). On the other hand, bending modes go like change in volume squared; for a membrane the change in volume is tiny since the membrane height is much less than its extension in the remaining directions [7]. Thus a deformed membrane tends to bend rather than stretch, and it is reasonable to assume surface area is conserved. The surface tension, Σ is often introduced as a Lagrange multiplier to enforce the conservation of surface area.

Just as one does to generate the MF Hamiltonian, Helfrich wrote down all energy terms consistent with the bending and stretching of a membrane [8]. Then specifics of the system determine the (ir)relevance and magnitude of various terms. As introduced in IIB2 (Eq. 5), there are two types of curvature which cost the membrane bending energy. Assuming different bending moduli for each curvature, the free energy for a patch of area on the membrane is [8]

$$\beta \mathcal{H} = \int dA \left[\frac{\kappa}{2} (2H)^2 + \bar{\kappa} K \right]. \tag{10}$$

By the Gauss-Bonnet theorem the last term in Eq. 10 contributes only a constant to the free energy if the topology of the surface does not change [2]. Assuming small fluctuations in the membrane ensures constant topological genus and allows the mean and Gaussian curvatures

to be written in terms of $h(\vec{x})$ [5]:

$$2H = \kappa_1 + \kappa_2 = \partial_{\alpha}^2 h(\vec{x})$$

$$K = \kappa_1 \kappa_2 = (\partial_1^2 h(\vec{x})(\partial_2^2 h(\vec{x})) - (\partial_1 \partial_2 h(\vec{x}))^2$$
(11)

We may also expand

$$dA = d^2x\sqrt{1 + (\partial_{\alpha}h)^2} \approx d^2x\left(1 + \frac{1}{2}(\partial_{\alpha}h)^2\right).$$

So with this approximation we disregard the Gaussian curvature term and penalize changes in surface area using Σ , arriving at Helfrich's free energy expresion:

$$\beta \mathcal{H}(h) = \frac{1}{2} \int d^2x \left[\kappa \left(\partial^2 h \right)^2 + \Sigma \left(\partial_\alpha h \right)^2 \right]. \tag{12}$$

Just as in the elastic formalism, free energy depends only on the bending and the change in area. Additional terms are easily appended to this expression to describe a closed vesicle with internal pressure, external forces, etc.

The Helfrich free energy can also be obtained in terms of the metric tensor by converting $dA \to d^2x\sqrt{\mathbf{g}}$ with $\mathbf{g} = \det g_{\alpha\beta}$. In the metric tensor formalism Eq. 12 is

$$\beta \mathcal{H} = \int d^2x \sqrt{\mathbf{g}} \left[r + 2\kappa H^2 + 2\bar{\kappa}K \right]$$
 (13)

with r a surface tension. The Gaussian curvature still contributes only a constant to the free energy.

C. Extrinisic curvatures

If the sheet is curved at zero temperature, the deviations from the natural parameterization, $g_{\alpha\beta}^0$, should be penalized. The penalty can be introduced by redefining the strain tensor (Eq. 7),

$$u_{\alpha\beta}(\vec{x}) = \frac{1}{2t_0^2} \left(g_{\alpha\beta}(\vec{x}) - g_{\alpha\beta}^0(\vec{x}) \right), \tag{14}$$

 t_0 being the MF value of the tangent vector in the unperturbed metric [9]. Alternatively the energy penalty can be introduced directly to the bending rigidity (κ) term (as in David's chapter 7.4 of [2]) so that,

$$\beta \mathcal{H}_{bending}(h) = \frac{\kappa}{2} \int dA \left(\partial^2 h - H_0 \vec{n} \right)^2 \tag{15}$$

with H_0 the mean curvature and $\vec{n}(\vec{x})$ the normal vector on the unperturbed membrane. When used to represent spontaneous curvature these representations (14 or 15) have equivalent effects on the bending term and do not influence any other relevant terms in the Hamiltonian. (Other types of quenched disorder could couple to strain terms in the Hamiltonian [9].)

Incorporating a spontaneous curvature into the Helfrich free energy (Eq. 10) gives

$$\beta \mathcal{H} = \int dA \left[\frac{\kappa}{2} (2H - C_0)^2 + \bar{\kappa} K \right]$$
 (16)

which is the expression Helfrich wrote in 1973 [8].

IV. THERMAL FLUCTUATIONS

A. Capillary waves

The deformations $h(\vec{x})$ can be written in terms of Fourier modes:

$$h(\vec{x}) = \int \frac{d^2q}{(2\pi)^2} e^{i\vec{q}\cdot\vec{x}} h(\vec{q}).$$

Then Eq. 12 becomes

$$\beta \mathcal{H} = \frac{1}{2} \int \frac{d^2 q}{(2\pi)^2} \left[\kappa q^4 + \Sigma q^2 \right] \left| h(\vec{q}) \right|^2 \tag{17}$$

which reveals the fluctuation correlations are

$$\left\langle \left| h(\vec{q}) \right|^2 \right\rangle = \frac{k_B T}{\kappa q^4 + \Sigma q^2}.$$
 (18)

In real space the average fluctuations are

$$\left\langle \left| h(\vec{x}) \right|^2 \right\rangle = \int \frac{d^2q}{(2\pi)^2} \frac{k_B T}{\kappa q^4 + \Sigma q^2}$$
 (19)

Thus fluctuations about a nearly-flat membrane are dominated by surface tension. This indicates that for long wavelength modes (small q) which occur at low temperatures, the fluctuations diverge as q^{-2} , or linearly with the area of the membrane. However, in the limit of vanishing surface tension (as is the case for most bilayer membranes) the bending terms are most relevant and fluctuations diverge as q^{-4} . By measuring these fluctuations it is possible to determine the effective bending rigidity κ . Experiments like this are discussed in VA.

B. Renormalization of the bending parameter

Beginning with the Hamiltonian for a nearly-flat elastic sheet from Eq. 9 and neglecting the nonlinear terms from the strain tensor in Eq. 8, the in-plane deformation modes decouple into \vec{u}_{\parallel} and \vec{u}_{\perp} so that in terms of normal modes, $\beta\mathcal{H}$ is

$$\beta \mathcal{H}(h, \vec{u}) = \frac{1}{2} \int \frac{d^2 q}{(2\pi)^2} \left[\kappa q^4 |h(\vec{q})|^2 + \frac{2\mu + \lambda}{4} q^4 |h(\vec{q})|^4 + \mu q^2 |\vec{u}_{\perp}(\vec{q})|^2 + (\mu + \lambda) q^2 |\vec{u}_{\parallel}(\vec{q})|^2 \right].$$
(20)

For a fluid membrane $\mu \to 0$ as discussed in the introduction, so the transverse modes are suppressed and $h(\vec{q})$ is only coupled to the longitudinal phonon modes. Nelson and Peliti [10] demonstrated that the remaining parallel phonon modes can simply be shifted such that $\lambda u'_{\alpha\alpha}^2 = \lambda \left[\partial_{\alpha} u_{\alpha} + (\partial_{\alpha} h)^2/2\right]^2$:

$$\beta \mathcal{H}_{fluid}(h, \vec{u}'_{\parallel}) = \frac{1}{2} \int \frac{d^2q}{(2\pi)^2} \left[\kappa q^4 |h(\vec{q})|^2 + \lambda q^2 |\vec{u}'_{\parallel}(\vec{q})|^2 \right]$$
(21)

Upon integrating out the phonon modes, one is left with a Gaussian theory for an effective $h'(\vec{x})$ with the same κ as before. Thus in the linear limit the bending rigidity is not renormalized because of the shift symmetry in $h(\vec{x})$.

In actuality the bending rigidity is renormalized by the inclusion of nonlinear phonon terms coupling the transverse and longitudinal phonon modes. The renormalization is calculated perturbatively by assuming the nonlinear terms are small compared to the Gaussian part. Peliti and Leibler [11], and David in Chapter 7.4 of [2] computed this renormalization to one-loop and found that in physically interesting dimensions (a 2D membrane embedded in 3D space) the bending rigidity is decreased by fluctuations (i.e. a membrane with wrinkles is easier to bend than a flat membrane). To first order in the perturbation theory, the spontaneous curvature, Gaussian rigidity, and surface tension are also renormalized.

Alternatively a variational method can be employed by using a trial Hamiltonian and minimizing the (Helfrich) free energy with respect to trial parameters. The variational approach is particularly useful for closed membranes with internal pressure or membranes with strong curvature, such as vesicles or biological cells. This method reveals extrinsic curvature can stiffen a membrane, e.g. small vesicles with large curvature have smaller fluctuations than larger vesicles [12, 13].

C. Rayleigh instability

Using the Helfrich formalism we can study thermal fluctuations on the surface of a cylindrical membrane. The unperturbed radius of the cylinder is R_0 , and the membrane has azimuthal symmetry. Principal curvatures are $\kappa_{\theta} = R_0^{-1}$ and $\kappa_z = 0$. Then fluctuations ρ in the radius of the membrane are functions of the length coordinate z. The perturbed principal curvatures are

$$\kappa'_{\theta} = \frac{1}{R(1 + (\partial_{\theta}\rho)^2)^{1/2}}, \quad \kappa'_{z} = -\frac{\partial_{z}^{2}\rho}{(1 + (\partial_{z}\rho)^2)^{3/2}}$$

so for small fluctuations the mean curvature $H \approx \frac{1}{R}$. The perturbations therefore do not significantly change the bending free energy (Eq. 15) [14], and perturbations' free energy is dominated by surface tension terms. By volume conservation the perturbed radius

$$R(z) \approx R_0 \left(1 - \frac{\rho(z)^2}{2R_0^2} \right).$$

Adapting Eq. 12, the unperturbed free energy is

$$\beta \mathcal{H}(\rho) = \frac{\Sigma}{2} \int d\theta dz R_0 = \Sigma \pi R_0 L \tag{22}$$

as expected, with L, the length of the cylinder, assumed to be much larger than R_0 . Including (small) fluctuations

the free energy is

$$\beta \mathcal{H}(\rho) \approx \frac{\Sigma}{2} \int d\theta dz R(z) \left(1 + \frac{1}{2} (\partial_z \rho)^2 \right)$$

$$= \Sigma \pi R_0 L \left[1 + \frac{1}{2} \int dq \left(q^2 - \frac{1}{R_0^2} \right) |\rho(q)|^2 \right]$$
 (24)

so $\Delta \mathcal{F} \propto (q^2 - R_0^{-2})$, meaning the small q fluctuations which occur at low temperatures actually *lower* the free energy of the cylinder if $R_0 \ll L$ like we assumed [5].

The long wavelength modes are unstable, so thermal fluctuations place constraints on the size and shape of vesicles which can exist. This instability causes cylindrical vesicles to break into spheres; spheres' topology prevents them from bending without stretching [7, 15]. As we have seen stretching modes are much more costly than bending modes, so the spherical vesicles' curvature suppresses fluctuations.

V. CONNECTIONS TO SIMULATIONS AND EXPERIMENTS

A. Measuring bending rigidity

A membrane at equilibrium will optimize its shape so that, as mentioned in IIIB, the attractive forces in the membrane precisely balance the packing entropy of the molecules. While a monolayer membrane usually cannot achieve a truly minimal configuration (e.g. due to interactions of the hydrophobic tails with water), a bilayer membrane can have vanishing surface tension (minimal free energy per area) since the membrane is free to compress or expand as necessary [16].

Thermal fluctuations of membranes can be measured using various mechanical or optical imaging techniques [17]. Thus one can measure the averages in Eqs. 18, 19 with good resolution when $q \approx \pi/L$, i.e. when fluctuations are roughly the size of the system. With excellent imaging contrast, one could also study short wavelength fluctuations and thereby possible membrane defects such as protrusions of individual molecules [18].

Comparing the experimentally measured fluctuation spectra to predicted profiles, the bending rigidity κ can be easily extracted when the surface tension of the membrane vanishes. In this way the effective bending rigidity is measured in various environmental conditions. Simulations are then used to probe phenomenological contributions of nonlinear phonon modes [19], protrusions [20], and chemical anistropies [21] to the renormalization of the bare bending rigidity. The simulations coupled with experimental measurements of κ reveal the relative weight of various corrections.

B. Vesicle size and shape distribution

As was demonstrated in IVC, thermal fluctuations tend to break up structures formed by membranes unless the fluctuations are suppressed by properties like spontaneous curvature or quenched/random defects in the membrane. Thus by determining the size and shape distributions of vesicles, and the conditions under which they become unstable, models are reverse-engineered to describe the (de)stabilizing features of a membrane.

For example, [13] proposes a model in which nonlinear elasticity terms renormalize the bending rigidity as a function of the (unknown) length scale at which the nonlinear terms become negligible. The authors then find that for some nonzero length scale simulations predict a distribution of vesicle size which matches experimental, equilibrated distributions of artificially generated vesicles. This suggests the nonlinear elastic terms play a role in destabilizing vesicles of a specific size, and points to a characteristic length scale for nonlinear term relevance.

There are other experiments which fix a membrane then perturb it with thermal fluctuations, pressure changes, or chemical processes. These perturbations prompt the formation of spontaneous curvatures or tubules which can remain stable once created or fragment from the base membrane [12]. These experiments inform theoretical models for flat membranes perturbed far from equilibrium, which can also be tested through simulations of anisotropy or random disorder in the membrane [15, 22]. Experimental probes of membrane sturdiness reveal the role of environmental or chemical stresses in catalyzing instability, with the goal of eventually engineering destabilizing processes.

VI. CONCLUSIONS

Using mean field theory and differential geometry, we constructed a model for (fluid) elastic membranes. Then by including thermal fluctuations we saw correlations in fluid membranes diverge linearly with the area, except in the special case of vanishing surface tension when the fluctuations diverge as q^{-4} . Unlike for solid membranes, thermal fluctuations do not renormalize the bending parameter to first order; nonlinear elasticity modes must be included to renormalized rigidity of a fluid membrane. A one-loop correction reveals fluctuations cause the membranes bending modes to soften (rather than stiffen as is the case for solid membranes). The effective rigidity can be measured experimentally and inform models as to the role of surface tension or membrane defects in renormalizing the couplings.

Imparting extrinsic curvature to the membrane alters its tolerance to thermal fluctuations. While some configurations (cylinder) are easily destroyed by low temperature fluctuations, other configurations (spheres) suppress fluctuations to stabilize the structure. Thus at ambient temperatures membranes may fragment into sta-

ble configurations based, again, on the chemical properties, anisotropies, and defects of the perturbed membrane. Observing the produced (simulated or physical) distribution of stable fragments lends insight to the relative magnitude of free energy contributions and relevant length scales in the model.

The investigation of fluid membrane fluctuations is much more interesting when membranes are layered. In fact, this much more accurately represents biological membranes such as lipid bilayers which are comprised of two tethered fluid elastic sheets. The effective couplings between layers reintroduce a shear modulus, and potentially a spontaneous curvature or effective surface tension. Bilayer membranes can also undergo thickness fluctuations as well as the height fluctuations we considered. These additional properties mean bilayer fluid membranes are more complicated to study analytically in the elastic formalism. However, systems with bilayer membranes are readily available for experimental studies, and are well-described by the Helfrich free energy with additional terms appended.

The transition from fluctuation-induced instability to fragmentation is a particularly interesting and active research area. A thorough understanding of the dynamical process, and ability to predict the shape and size of final structures, has promising applications in medical and industry settings. Of particular interest for biologists are processes involving topological deformations (such as endocytosis and budding) which are instigated by environmental cues and stresses. These processes alter the genus of the membrane, meaning the Gaussian curvature (K) term contributes nontrivially to the free energy. Contributions from changing topology and external (active) forces (e.g. from proteins in the cell) should be investigated to obtain a complete picture of these commonplace, yet theoretically elusive, biological processes.

ACKNOWLEDGEMENTS

Thank you to Prof. Mehran Kardar for a great textbook and pristine lectures throughout the semester; to Cris Zanoci for hints and discussions about assignments and well-planned recitations; and to Prof. Ariel Amir for suggesting an interesting and fun final project topic.

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